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RESEARCH ARTICLE

Environmental factors affecting the success of exotic plant invasion in a wildland-urban ecotone in temperate South America

Fatores ambientais que afetam o sucesso da invasão de plantas exóticas no ecótono urbano-silvestre

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Abstract

Urbanization is one of the main causes driving changes in biodiversity patterns and it is regarded as a major threat to native biota. Successful exotic plant invasion depends on invasiveness and invasibility. Invasiveness is related to the characteristics of exotic plants and invasibility to the features of the sites. The objective of this study was to identify the invasibility environmental factors affecting the success of exotic plant invasion in a wildland-urban ecotone of the central region of Argentina (Potrero de los Funes Village, San Luis). Fifty phytosociological inventories were recorded in an area of 700 ha during spring and summer seasons (2013–2015). Abundance-coverage values of plants and environmental variables such as soil characteristics, anthropogenic disturbance, and altitude of the sites were assessed. Soil moisture, electrical conductivity (EC), acidity (pH), organic matter content, and nitrates were determined as part of the soil analysis. A Nonmetric Multidimensional Scaling analysis was used to identify the possible relationship between abundance-coverage of the vegetation and environmental variables. Abundance-coverage of exotic plants was positively influenced by anthropogenic disturbance and nitrate levels, and negatively affected by altitude. However, no significant correlation was found between percentage of exotic plants and pH, EC, or soil moisture. Thus, urbanization and touristic activities influenced the success of exotic plant invasion.

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PENSOFT.

Resumo

A urbanização é uma das principais causas das mudanças nos padrões de biodiversidade sendo considerada uma grande ameaça à biota nativa. O sucesso exitoso da invasão das plantas exóticas depende da invasividade e invasibilidade. A invasividade está relacionada com às características das plantas exóticas e à invasibilidade com às características dos locais. O objetivo deste estudo foi identificar os fatores ambientais de invasibilidade que afetam o sucesso da invasão das plantas exóticas em ecótono urbano-silvestre na região central da Argentina (Potrero de los Funes, San Luis). Cinquenta inventários fitossociológicos foram registrados em uma área de 700 ha durante as estações primavera e verão (2013–2015). Valores de cobertura-abundância das plantas e variáveis ambientais, como características do solo, perturbação antropogênica e altitude dos sítios foram avaliadas. A umidade do solo, condutividade elétrica, acidez (pH), conteúdo de matéria orgânica e nitratos foram determinados como parte da análise do solo. Uma análise de escalonamento multidimensional não-métrico foi utilizada para identificar a possível relação entre a cobertura de abundância da vegetação e as variáveis ambientais. A abundância-cobertura de plantas exóticas foi positivamente influenciada pelas perturbações antrópicas e os níveis de nitrato e negativamente afetada pela altitude. No entanto, nenhuma correlação significativa foi encontrada entre a porcentagem de plantas exóticas e pH, EC ou umidade do solo. Assim, a urbanização e atividades turísticas influenciaram o sucesso da invasão de plantas exóticas.

Keywords

altitude, anthropogenic disturbance, invasibility, soil characteristics

Palavras-chave

altitude, características do solo, distúrbio antropogênico, invasibilidade

Introduction

Successful exotic plant invasion depends on invasiveness and invasibility. Invasiveness is related to the characteristics or biological traits of exotic plants (Rejmánek and Richardson 1996; Keane and Crawley 2002), whereas invasibility is related to the features of the sites (Lonsdale 1999). Invasibility plays a key role in the success of invasion. Lee (2001) reported that invasibility explains 60% of the success of invasive plants, while invasiveness only explains 12% of the process. Therefore, habitat characteristics are important predictors and drivers of successful invasions and are also relatively easy to measure (Stohlgren et al. 2001). Given the increasing change in land use, due to urban and suburban development in or near wildland vegetation, it is important to understand how human activities are altering both biodiversity and ecosystem functioning (Tylianakis et al. 2008). It is widely accepted that the disturbance regime of an area is involved in the success of invasion by exotic plants (Mack et al. 2000; Xiao et al. 2016). Numerous studies have suggested that invasive plant distribution is closely related to anthropogenic influences, including housing development, proximity to roads, agriculture and socioeconomic factors such as income (Ariori et al. 2017). Thus, invasive species are expected to be more common in places with a long history of human development, close to urban centers, high density of roads, and in areas designated for agricultural and grazing activities (Ghersa et al. 2002; Pauchard and Alaback 2002).

Several soil characteristics have been associated with plant invasion (Elton 1958; Stohlgren et al. 1999, 2006; Fridley et al. 2007). Nitrates (Ross et al. 2011), organic matter (Knicker et al. 2000), pH (Ehrenfeld 2003; Stohlgren et al. 2003; Hill et al. 2005; Hegazy et al. 2008), and electrical conductivity (Perelman et al. 2007; Hegazy et al. 2008) are the most widely studied. Invasive plant success has also shown a relationship with latitude and altitude mainly due to extreme climate conditions. Cold environments at higher elevation and higher latitude often present distinctive biodiversity and are considered resistant to biological invasions (Pauchard and Alaback 2002; Pyšek and Richardson 2006; Pauchard et al. 2016). Finally, invasibility success has been associated with the proximity to riparian habitats (Stohlgren et al. 1999; Richardson et al. 2007; Ringold et al. 2008).

The province of San Luis, Argentina is characterized by a low industrial development in contrast with accelerated urban growth (Calderon et al. 2017). Specifically, the total population of Potrero de los Funes Village has increased from 410 to 1698 which is equivalent to a 300% population increase in the last 25 years (Instituto Nacional de Estadística y Censos 2010), and this has been accompanied by the constant expansion of infrastructure. Potrero de los Funes also experiences a high influx of tourists year round, with the highest concentration during the summer season due to the presence of a river that flows through the town (Potrero de los Funes River). Thus, this area constitutes the perfect site for the study of exotic plant invasibility within an anthropogenically disturbed ecosystem. This investigation provides the first insight regarding the relationships between exotic plant success and site characteristics in a natural-urban gradient ecosystem of the central area of Argentina. Information about the environmental factors influencing the distribution of exotic species at a local scale is the first step in order to predict the potential of exotic plants expansion at regional scale and the threat that these invasions pose to native biota.

The objective of this study was to identify the invasibility environmental factors affecting the success of exotic plant invasion in a wildland-urban ecotone. We hypothesize that the abundance-coverage of exotic plants is positively influenced by high soil moisture, organic matter content, nitrate concentration, neutral pH, and anthropogenic disturbance. Even when these hypotheses have been broadly tested, mainly in Europe and other parts of the Northern Hemisphere, this is the first study performed in the biographic Chaco Serrano District. We also hypothesize that the abundance-coverage of exotic plants is negatively influenced by high electrical conductivity and altitude.

Methods

Study area

The village of Potrero de los Funes is located in the southwest portion of the Sierras de San Luis System in San Luis province, central region of Argentina (Fig. 1). The Sierras de San Luis System is a hilly area that reaches 160 km long (east to west

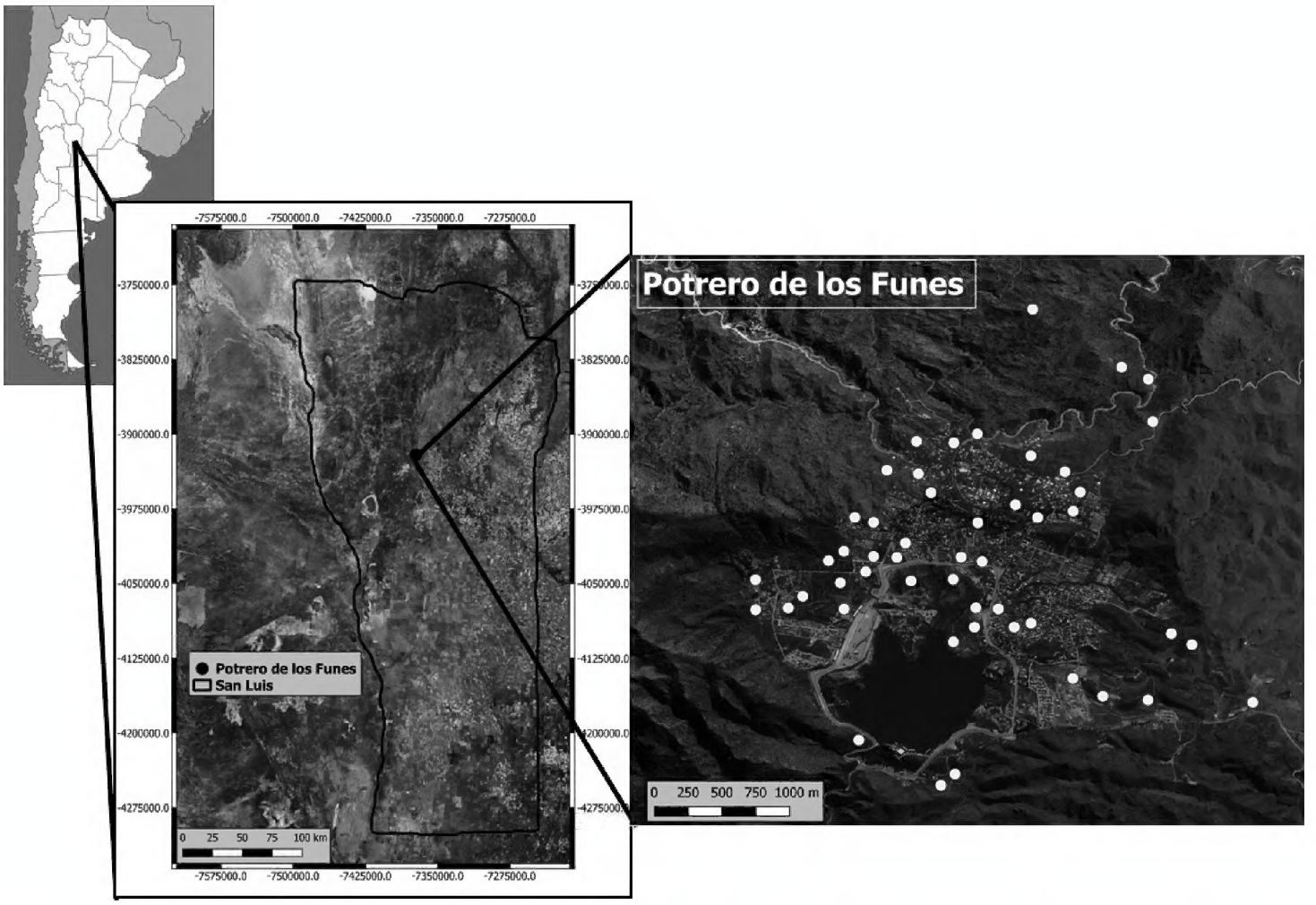

Figure 1. Locations of the 50 plots in Potrero de los Funes Village, San Luis province, central region of Argentina, used for soil sampling and phytosociological inventories during spring and summer seasons from 2013–2015.

oriented) with an average height of 1500 m a.s.l. Climate is mesotermic and dry subhumid (Thornthwaite 1948), with an average annual rainfall of 600 mm. Biogeographically, the area of study is located within the Chaqueño Serrano District of the Chaco Province (Cabrera 1976). The vegetation is presented as a mosaic with clear differences due to the local environmental characteristics and land use that shape the landscape. In the most-preserved areas of this Chaqueño Serrano District, the vegetation is represented primarily by woodland dominated by *Lithraea molleoides* while in the more degraded areas the vegetation changes to shrubland dominated by Fabaceae, Poaceae, and forbs (Cabrera and Willink 1980). This area is characterized by a high urban and touristic influx with no agriculture, industrial or mining activities developed in the surroundings.

Anthropogenic disturbance index

An anthropogenic disturbance index was used to evaluate the level of anthropogenic disturbance of each site (Nievas and Moglia 2014). This index takes into account factors related to several types of anthropogenic disturbances such as mining, agriculture, and industrial activities. However, most of the items assessed through this index are associated with urban development (Table 1). Twenty-three items were evaluated qualitatively in a scale as follows: 0 (null), 1 (low), 2 (medium), 3 (high).

Table 1. The 23 anthropogenic disturbance factors assessed in order to estimate the degree of human disturbance surrounding each site in Potrero de los Funes, San Luis province, central region of Argentina.

Anthropogenic disturbance index	
Cattle faeces	Water extraction pipes
Stray animals, breeding centres	Mining activity
Overgrazing	Dams, reservoirs
Agricultural areas	Channelization
Clearing, wood extraction	Stormwater/sewer drainage pipes
Construction debris	Diverted channels
Soil Erosion	Isolated channels
Density of houses	Presence of gabions
Proximity to city/town	Bridges
Human trails and gravel/dirt roads	Landfill, urban solid waste disposal areas
Paved roads	Others
Constructions for recreational purposes	
Evidence of fires	

The score for each item was determined by comparison among sites with the same operator conducting the assessment in order to avoid differences in criteria. The values for every factor were summed to obtain the final score for each site.

Soil sampling

Four soil samples were taken from the root zone with a 6 cm diameter cylinder and within the 10–30 cm in depth in each plot. Measured soil parameters included gravimetric moisture, electrical conductivity (EC) and pH, evaluated in 1:5 (by weight) soil-water extract using an EC meter and pH meter, respectively. Organic matter was determined through the Walkley and Black's method and nitrates were evaluated by chromotropic acid method (Padilla and Olivera 1991). Soil and phytosociological inventories were carried out at the same dates.

Vegetation sampling

Satellite images were used to identify homogenous vegetation areas and the number of plots needed to perform a representative vegetation survey of the study area (700 ha). Fifty plots were established at random. Plot size was determined for each vegetation type using the minimal area method, meaning that the plot had to be large enough to represent community composition (Braun-Blanquet 1913). Vegetation plots were located at a maximum altitude of 1099 m a.s.l. due to the difficulty of access. Phytosociological inventories were performed and abundance-coverage values of taxa were recorded in order to identify patterns in the distribution of the species (Mueller-Dombois and Ellemberg 1974; Matteucci and Colma 1982). The plots were named after the dominant species present. Data were collected from 2013 to 2015 during the spring and summer seasons, which corresponded with the reproductive stage of most plants in the area. The species that could not be identified

in the field were taken to the laboratory for taxonomic identification using botanical catalogs (Zuloaga et al. 1994; Zuloaga and Morrone 1996; Zuloaga and Morrone 1999) and in accordance with the Instituto de Botánica Darwinion (Instituto de Botánica Darwinion 2014).

Data analysis

Two data matrices representing environmental variables and vegetation abundance-coverage were constructed and the PC-ORD 5.0 software package was used for multivariate statistical analysis (Non-metric Multidimensional Scaling; NMDS) (Holt et al. 2009). NMDS was used to identify environmental variables related with the patterns of vegetation distribution, meaning the distribution of abundance-coverage of exotic species within the plots and communities. NMDS is an indirect ordination technique and an iterative method of sorting and, summarizing the multivariate relationships among sites. Environmental variables that were not significant contributors to explain the vegetation patterns were excluded from the final diagram (Chahouki 2013). In addition, Spearman's correlation analysis was used to evaluate the relationship between the stronger environmental variables identified by the NMDS and percentage exotic plants at each site. Correlations were only accepted if $p \leq 0.01$.

Results

Anthropogenic disturbance, altitude, and soil characteristics

The anthropogenic disturbance index varied among plots from values below 10 for the most preserved plots (ESPIN, MOLLE, CORTA) to values close to 20 for the most disturbed plots (CYNO, CARDA, CARDALCA). The altitude of the sites ranged from 911 m a.s.l. (CYNO1) to 1099 m a.s.l. (SOPHO11). Soil chemical characteristics also varied among plots, mainly in the nitrate content (Table 2).

Vegetation analysis

Fifty phytosociological inventories were performed at the area of study (see Suppl. material 1: Phytosociological inventories). A total of 105 species were identified during the field assessments, 27 species were exotic, and 78 were native (Table 3).

The percentage of exotic plants species within the plots varied from 0% in the most preserved sites (ESPIN, SOPHO, CHILFLO) to 70% in the most disturbed sites (CARDA, CARDALCA). The abundance-coverage of exotic species also varied among plots with some dominated by exotics (CARDA, CYNO, HETERO). The minimum stress of the three axes in the NMDS ordination was 17.9. As part of the NMDS analysis, the Monte Carlo test showed a $p = 0.004$ and the instability was 0.00386 in 500 iterations. The first three ordination axes explained a cumulative 60%

Table 2. Anthropogenic Disturbance Index values, altitude and soil chemical parameters (average ± standard error) at the plots in Potrero de los Funes, San Luis province, central region of Argentina.

Plot ID	Anthropogenic disturbance index	Altitude (m a.s.l.)	Soil moisture (%)	EC ($mS \cdot cm^{-1}$)	pH	Organic matter (%)	Nitrates (ppm)
ESPIN1	7	979	2.20±0.002	0.6±0.12	6.95±0.06	0.7±0.02	13.8±0.25
ESPIN2	8	997	2.20±0.0015	0.6±0.1	6.95±0.07	0.7±0.03	12.2±0.28
ESPIN3	8	920	0.80±0.002	1.35±0.13	7.97±0.1	0.45±0.01	13±0.31
ESPIN4	7	1009	2.20±0.03	0.6±0.12	6.95±0.05	0.7±0.02	13.2±0.45
ESPIN5	7	978	2.20±0.03	0.6±0.1	6.95±0.1	0.7±0.032	13.3±0.19
ESPIN6	8	980	2.54±0.002	0.22±0.1	7.42±0.07	0.81±0.01	12±0.18
ESPIN7	6	998	1.61±0.0041	0.23±0.1	5.47±0.07	0.81±0.02	12.6±0.27
ESPIN8	9	999	2.20±0.002	0.6±0.12	6.95±0.1	0.7±0.025	11±0.21
BC2	11	967	17.16±0.01	0.53±0.08	6.54±0.1	1.18±0.01	31±0.8
BC1	11	968	17.20±0.01	0.54±0.07	6.44±0.1	1.2±0.01	28±0.7
CHILFLO1	12	962	8.55±0.02	0.7±0.07	5.57±0.06	1.2±0.005	13.5±0.31
CHILFLO2	10	992	8.55±0.04	0.6±0.05	5.5±0.05	1.21±0.01	9±0.2
CHILFLO3	12	969	2.70±0.03	0.69±0.07	5.7±0.05	1.19±0.01	12±0.3
CHILFLO4	11	994	8.55±0.04	0.65±0.05	5.6±0.06	1.22±0.01	10.2±0.27
CORTA1	9	988	22.03±1.2	0.27±0.03	6.96±0.1	0.25±0.003	7.7±0.13
CORTA2	9	973	28.1±1.3	0.26±0.05	7±0.06	0.21±0.004	3.1±0.08
CORTA3	8	991	25.04±1.2	0.25±0.05	6.8±0.07	0.23±0.002	5.6±0.15
CORTA4	9	958	20.02±1.3	0.28±0.06	6.78±0.07	0.2±0.006	6.2±0.17
CORTA5	8	943	20.08±1.5	0.24±0.05	6.96±0.06	0.27±0.003	7±0.17
HETSAL1	9	968	5.9±0.1	0.3±0.05	7.61±0.1	1.1±0.002	28±0.89
HETSAL2	10	990	9.92±0.4	0.13±0.04	6.81±0.03	0.72±0.002	23±0.7
HETSAL3	10	963	4.1±0.3	0.28±0.05	8.71±0.05	0.31±0.002	26±0.65
HETSAL4	9	984	10.00±0.5	0.13±0.02	6.81±0.07	0.72±0.003	24.5±0.72
HETSAL5	10	964	10.02±0.4	0.14±0.01	7±0.07	0.71±0.005	28.2±0.68
HETSAL6	9	961	0.65±0.02	0.13±0.02	6.81±0.08	0.72±0.005	28.1±0.73
CARDA3	17	970	15.14±0.6	0.42±0.01	7.05±0.05	1.03±0.01	11.5±0.35
CARDA2	18	1039	15.14±0.7	0.48±0.02	6.95±0.1	1.05±0.01	13±0.25
CARDA1	18	1039	15.50±0.5	0.42±0.02	6.87±0.06	1.04±0.013	25±0.9
CARDALCA	20	964	15.16±0.4	0.41±0.01	7.01±0.07	1.03±0.015	22±0.61
CYNO1	17	911	0.8±0.003	1.35±0.06	7.97±0.1	0.45±0.03	31.5±0.82
CYNO2	18	955	4.1±0.05	0.28±0.01	8.71±0.13	0.31±0.02	28.8±0.75
CYNO3	18	976	10.00±0.5	0.25±0.01	7.96±0.15	0.44±0.02	32±0.65
CYNO4	19	984	9.95±0.5	0.23±0.02	7.89±0.11	0.49±0.03	30±0.77
CYNO5	18	963	9.00±0.4	0.25±0.01	8±0.1	0.47±0.02	29±0.91
MOLLE1	6	1028	3.30±0.2	0.14±0.01	6.87±0.09	0.26±0.01	14.8±0.4
MOLLE4	6	1083	3.19±0.3	0.28±0.01	6.29±0.07	0.64±0.02	39.1±0.7
MOLLE3	5	998	3.24±0.17	0.2±0.01	6.5±0.06	0.50±0.02	15±0.5
MOLLE2	6	971	3.20±0.2	0.28±0.02	6.29±0.06	0.64±0.023	13±0.45
TAGBID1	9	975	14.50±0.7	0.17±0.01	7.77±0.05	0.89±0.02	15.6±0.65
TEGBID2	8	962	13.60±0.5	0.25±0.01	7.96±0.07	0.44±0.02	12±0.51
TEGBID3	8	1099	25.00±0.8	0.21±0.01	7.66±0.05	0.5±0.022	22.5±0.48
TEGBID4	9	965	25.66±0.7	0.23±0.01	7.76±0.06	0.53±0.021	20±0.52
TEGBID5	8	991	15.66±1.2	0.21±0.02	7.69±0.07	0.52±0.03	15±0.56
SOPHO8	4	970	10.56±0.8	0.17±0.02	6.99±0.05	0.98±0.01	12.65±0.36
SOPHO11	5	1011	11.00±0.62	0.15±0.01	7.1±0.08	0.96±0.02	12±0.37
POLYXAN1	12	959	16.12±0.6	0.083±0.001	5.55±0.08	1.11±0.016	13.5 6±0.4
POLYXAN2	11	965	5.65±0.34	0.093±0.002	5.65±0.07	1.21±0.01	15±0.38
HETERO1	10	964	7.29±0.41	0.4±0.01	6.95±0.09	1.02±0.01	15.6±0.41
HETERO2	9	948	7.70±0.5	0.42±0.02	7.09±0.05	1.12±0.01	22.3±0.6
HETERO3	12	954	7.50±0.3	0.44±0.01	6.98±0.07	1.52±0.016	25.6±0.7

Table 3. Species list of 105 taxa registered during the phytosociological inventories performed in Potrero de los Funes, San Luis province, central region of Argentina, from 2013–2015. Exotic species are indicated in bold.

Species	Code	Species	Code
Abutilon grandifolium (Willd.) Sweet	abugra	*Jodina rhombifolia* (Hook. & Arn.) Reissek	jodrho
Acalypha poiretii Spreng.	acapoi	*Justicia tweediana* (Nees) Griseb.	justwe
Acanthostyles buniifolius (Hook. & Arn.) R.M. King & H. Rob.	acabun	*Lantana grisebachii* Stuck. ex Seckt	langri
Aloysia gratissima (Gillies & Hook. ex Hook.) Tronc. var. *gratissima*	alogra	*Leptochloa crinita* (Lag.) P.M. Peterson & N.W. Snow	lepcri
Amelichloa brachychaeta (Godr.) Arriaga & Barkworth	amebra	*Lippia junelliana* (Moldenke) Tronc.	lipjun
Anemia tomentosa (Savigny) Sw.	anetom	*Lithraea molleoides* (Vell.) Engl.	litmol
Baccharis artemisioides Hook. & Arn.	bacart	*Lorentzianthus viscidus* (Hook. & Arn.) R.M. King & H. Rob.	lorvis
Baccharis flabellata Hook. & Arn.	bacfla	*Malvastrum* sp.	malvas
Baccharis salicifolia (Ruiz & Pav.) Pers.	bacsal	***Medicago lupulina* L.**	**medlup**
Baccharis sp.	rombac	*Melica macra* Nees	melmac
Baccharis ulicina Hook. & Arn.	baculi	***Melilotus albus* Desr.**	**melalb**
***Bassia scoparia* (L.) A.J. Scott**	**bassco**	***Morus alba* L.**	**moralb**
Bidens pilosa L.	bidpil	*Nassella tenuissima* (Trin.) Barkworth	nasten
Bidens subalternans DC.	bidsub	***Oenothera curtiflora* W.L. Wagner & Hoch**	**gaupar**
Bothriochloa springfieldii (Gould) Parodi.	botspr	*Oxalis conorrhiza* Jacq.	oxacon
Bouteloua curtipendula (Michx.) Torr.	boucur	*Pappophorum* sp.	paposp
Bowlesia incana Ruiz & Pav.	bowinc	*Paspalum dilatatum* Poir.	pasdil
Bromus catharticus Vahl	brocru	***Plantago major* L.**	**plamaj**
***Carduus acanthoides* L.**	**caraca**	***Poa annua* L.**	**poacsp**
***Carduus thoermeri* Weinm.**	**cartho**	***Polygonum persicaria* L.**	**polper**
Celtis tala Gillies ex Planch.	celehr	*Porlieria microphylla* (Baill.) Descole, O´Donell & Lourteig	pormic
Cestrum parqui L'Hér.	cespar	*Prosopis caldenia* Burkart	procal
Chaptalia sp.	chapsp	*Prosopis nigra* (Griseb.) Hieron.	pronig
Cheilanthes buchtienii (Rosenst.) R.M. Tryon	chebuc	***Prunella vulgaris* L.**	**pruvul**
***Chenopodium album* L.**	**chealb**	*Rhodoscirpus asper* (J. Presl & C. Presl) Léveillé-Bourret, Donadío & J.R. Starr	rhoasp
***Cirsium vulgare* (Savi) Ten.**	**cirvul**	***Rosa rubiginosa* L.**	**rosrub**
Clematis montevidensis Spreng.	clemon	*Schinus fasciculatus* (Griseb.) I.M.	schfas
Colletia spinosissima J.F. Gmel.	colspi	*Schizachyrium plumigerum* (Ekman) Parodi	schplu
Commelina erecta L.	comere	*Senna subulata* (Griseb.) H.S. Irwin & Barneby	sensub
Condalia microphylla Cav.	conmic	*Setaria lachnea* (Nees) Kunth	setlac
Cortaderia selloana (Schult. & Schult. f.) Asch. & Graebn.	corsel	*Setaria parviflora* (Poir.) Kerguélen	setpar
***Cosmos sulphureus* Cav.**	**cossul**	*Sida spinosa* L.	sidspi
***Cynodon dactylon* (L.) Pers.**	**cyndac**	*Solanum elaeagnifolium* Cav.	solela
Descurainia erodiifolia (Phil.) Prantl ex Reiche	desero	***Sonchus asper* (L.) Hill**	**sonasp**
Dichondra microcalyx (Hallier f.) Fabris	dicmic	***Sorghum halepense* (L.) Pers.**	**sorhal**
Eryngium horridum Malme	eryhor	*Sophora linearifolia* Griseb.	soplin
Euphorbia dentata Michx.	eupden	*Symphyotrichum squamatum* (Spreng.) G.L. Nesom	symsqu
Eustachys retusa (Lag.) Kunth	eusret	*Tagetes minuta* L.	tagmin

Species	Code	Species	Code
Evolvulus arizonicus A. Gray	evoari	***Taraxacum officinale* F.H. Wigg.**	**taroff**
Evolvulus sericeus Sw.	evoser	*Tarenaya aculeata* (L.) Soares Neto & Roalson	cleacu
Flourensia thurifera (Molina) DC.	floool	*Tessaria absinthioides* (Hook. & Arn.) DC.	tesabs
Galium richardianum (Gillies ex Hook. & Arn.) Endl. ex Walp	galric	***Trifolium repens* L.**	**trirep**
Galinsoga parviflora Cav.	galpar	*Typha domingensis* Pers.	typdom
Geoffroea decorticans (Gillies ex Hook. & Arn.) Burkart	geodec	***Ulmus* sp.**	**ulmusp**
Glandularia sp.	glalil	*Urtica circularis* (Hicken) Sorarú	urtcir
Heimia salicifolia (Kunth) Link	heisal	*Vachellia astringens* (Gillies ex Hook. & Arn.) Speg.	vacast
Heterosperma ovatifolium Cav.	hetova	*Vachellia caven* (Molina) Seigler & Ebinger	vaccav
***Heterotheca subaxillaris* (Lam.) Britton & Rusby**	**hetsub**	***Viola metajaponica* Nakai**	**viomet**
Hydrocotyle bonariensis Lam.	hydbon	***Viola odorata* L.**	**vioodo**
*Iresine diffu*sa Humb. & Bonpl. ex Willd	iredif	***Xanthium strumarium* L.**	**xanstr**
Ipomoea rubriflora O'Donell	iporub	***Xanthium spinosum* L.**	**xanspi**
Jarava pseudoichu (Caro) F. Rojas	jarpse	*Zinnia peruviana* (L.) L.	zinper
Jarava ichu Ruiz & Pav.	jarich		

of variance in the dataset. The ordination final diagram showed that the pattern of distribution of exotic plants was positively related with anthropogenic disturbance, nitrate, soil moisture, and pH, and it was negatively related with altitude. The ordination diagram separated plots according to these environmental variables (Fig. 2). Soil moisture and anthropogenic disturbance showed positive correlations with axis one ($r = 0.552$ and $r = 0.561$, respectively), whereas altitude showed a negative correlation ($r = -0.600$). A weak positive correlation was found between pH and axis two ($r = 0.504$). Nitrate showed a positive correlation with axis three ($r = 0.722$). No significant relationship among vegetation patterns, organic matter, and EC was found.

The following species were associated with axis 1: *Vachellia caven* ($r = -0.630$), *Cirsium vulgare* ($r = 0.491$), *Medicago lupulina* ($r = 0.472$), *Bouteloua curtipendula* ($r = -0.459$), and *Flourensia thurifera* ($r = -0.416$). The species associated with axis two were: *Xanthium spinosum* ($r = -0.572$), *Polygonum persicaria* ($r = -0.570$), *Xanthium strumarium* ($r = -0.535$), *Chenopodium album* ($r = -0.499$), *Bidens subalternans* ($r = 0.448$), and *Tagetes minuta* ($r = 0.419$). The species that were associated with axis three were: *Heterosperma ovatifolia* ($r = 0.607$), *Cynodon dactylon* ($r = 0.541$), *Salpichroa origanifolia* ($r = 0.521$), and *Cortaderia selloana* ($r = -0.519$) (Fig. 3). Species codes are explained in Table 3.

The plant communities related with higher altitudes were the ones dominated by "mollares" of *Lithraea molleoides*, "espinillares" of *Vachellia caven*, "chilcales" of *Flourensia thurifera*, and "soforales" of *Sophora linearifolia*. These plant communities were the most conserved and with the lowest percentages of exotic plants. These communities include the mature forest communities ("mollares") and their regressive succession stages: "espinillares" of *Vachellia caven*, "chilcales" of *Flourensia thurifera*, and "soforales" of *Sophora linearifolia*.

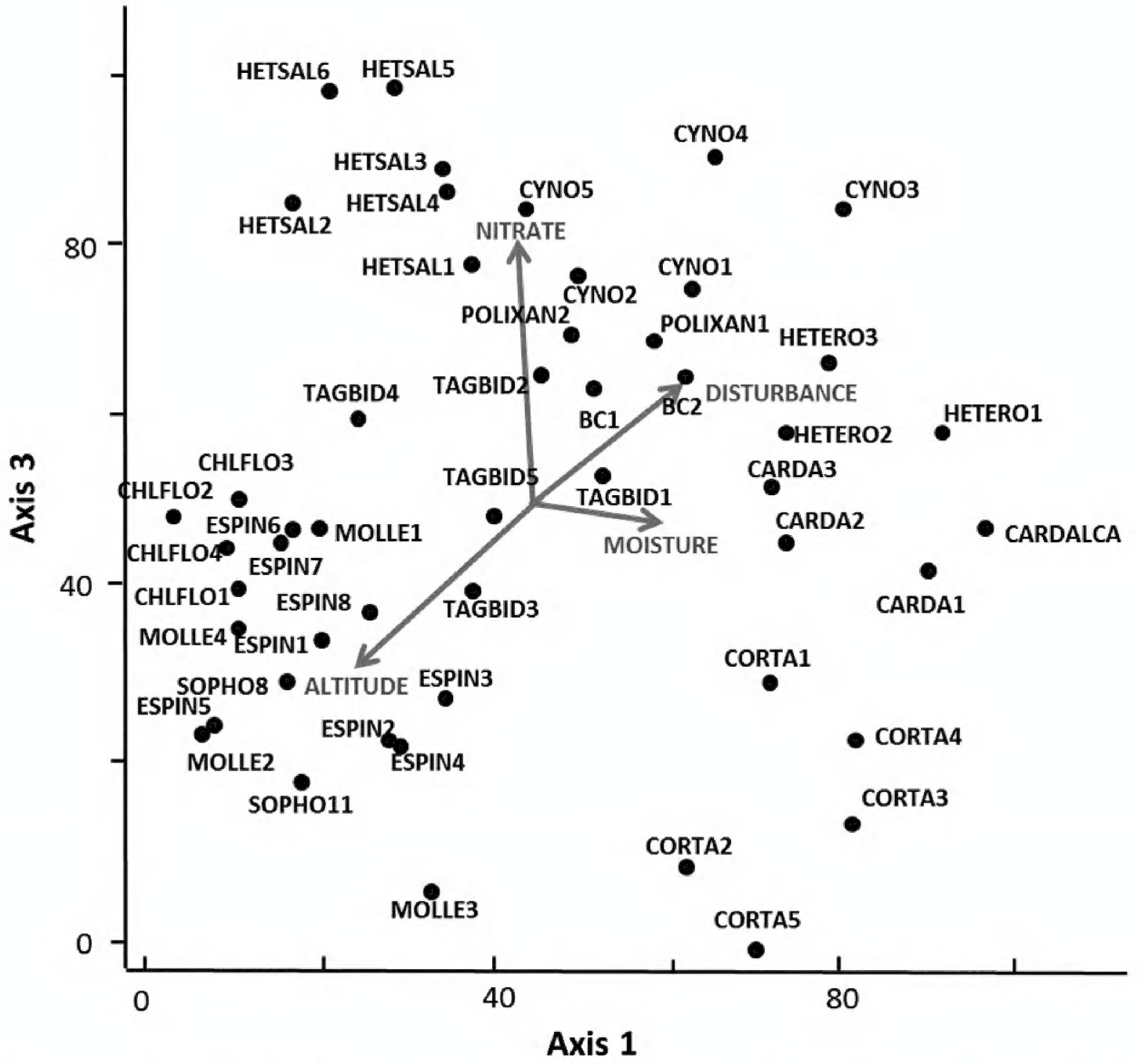

Figure 2. Plot ordination of non-metric multidimensional scaling (NMDS) based on the abundance-coverage data of plant species in Potrero de los Funes Village, San Luis province, central region of Argentina. Black dots represent the plots and the vectors the environmental variables related to NMDS axes (cutoff level $r^2 = 0.22$). The names of the plots are determined by the dominant species within the plot: ESPIN ("espinillares"of *Vachellia caven*), CHILFLO ("chilcales" of *Flourensia thurifera*), MOLLE ("mollares" of *Lithraea molleoides*), SOPHO ("soforales" of *Sophora linearifolia*), HETSAL (*Heterosperma ovatifolium* and *Salpichroa origanifolia,*), TAGBIB (*Tagetes minuta* and *Bidens subalternans*), CYNO (*Cynodon dactylon*), CORTA (*Cortaderia selloana*), CARDA and CARDALCA ("cardales" of *Cirsium vulgare*), BC (*Prosopis caldenia*), HETERO ("alcanforales" of *Heterotheca subaxillaris*).

Exotic plant communities dominated by *Heterotheca subaxillaris* ("alcanforales") and *Cirsium vulgare* ("cardales") were found at lower altitudes, with high concentrations of nitrate and high percentages of soil moisture. *Medicago lupulina*, *Cirsium vulgare*, *Cynodon dactylon*, *Chenopodium album*, and *Xanthium spinosum* were exotic species common in disturbed and nitrogen-enriched sites together with native species such as *Salpichroa origanifolia*, *Heterosperma ovatifolium*, and *Oxalis conorrhiza*.

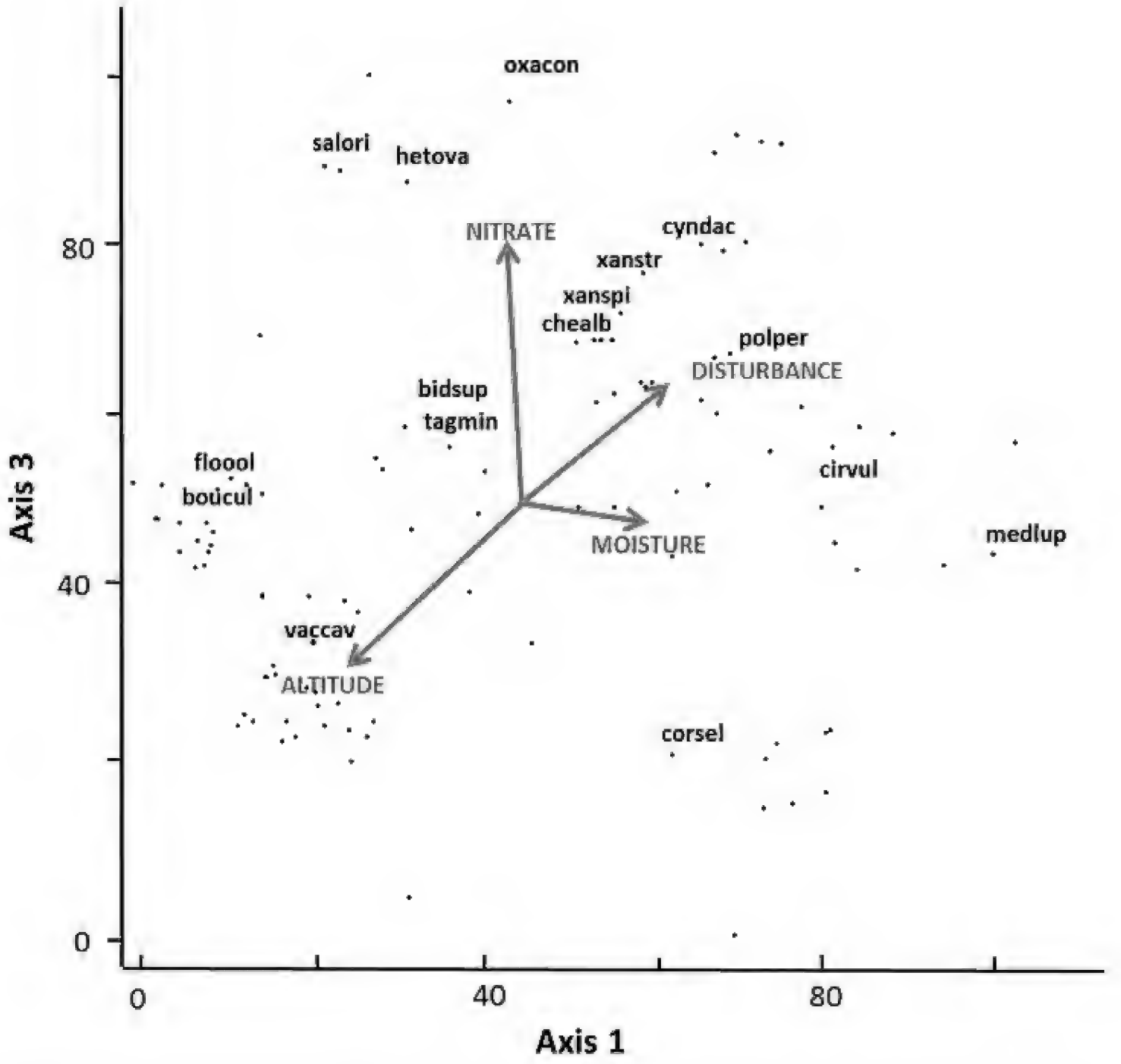

Figure 3. Species ordination of non-metric multidimensional scaling (NMDS) plot based on abundance-coverage data. Black dots represent the species and vectors of the environmental variables related to NMDS axes (cutoff level $r^2 = 0.22$). All 105 species were included in NMDS, but for clarity only the 16 most abundant species were plotted on the ordination final diagram.

Spearman's correlation test confirmed that anthropogenic disturbance was the variable most strongly correlated with the percentage of exotic plants ($r = 0.600$; $p < 0.00004$) followed by a moderate correlation with nitrate concentration on soil ($r = 0.500$; $p < 0.01$) and a negative correlation with altitude ($r = -0.400$; $p < 0.01$). No significant correlation was found between percentage of exotic plants and pH, EC, or soil moisture ($p > 0.01$).

Discussion

In accordance with the hypothesis established in this investigation, a strong positive relationship between anthropogenic disturbance and abundance-coverage of exotic

plants was found. Many researchers have arrived at similar conclusions and reported that anthropogenic disturbance is a key factor in invasion success (Richardson et al. 2007; Geneletti and Dawa 2009; Prasad 2009; Xiao et al. 2016; Ariori et al. 2017). For example, Hierro et al. (2005) concluded that humans were the main driver of the expansion of the distribution area of several organisms, including plants, as part of their analysis of the biogeographic basis of plant invasion. They stated that species taken from their native range and moved beyond their natural dispersal barriers can increase their abundance due to the influence of a different set of ecosystem characteristics. Moreover, Wu et al. (2010) studied the patterns of plant invasion in China and reported that anthropogenic factors, including demography and tourism, were strongly correlated with the intensity of exotic plant invasion. They determined that human intervention was largely responsible for creating opportunities for a successful exotic invasion at regional scale.

In the last three decades, the area of study has experienced an increase in population growth, urbanization, and tourism influx that may explain the success of invasion reflected in our results. Most of the exotic plants found in the area of study were intentionally introduced as ornamentals and for landscaping purposes around houses, camping areas and recreational establishments. Additionally, unintentional human-mediated dispersal through contaminated footwear and clothes along hiking trails within the area may contribute to the expansion of the exotic plant distribution (Geneletti and Dawa 2009). Thus, the degradation of the structure and composition of plant communities in Potrero de los Funes can be explained by the level of anthropogenic disturbance.

A positive relationship between nitrate concentration in soil and patterns in vegetation distribution was found. Spearman's correlation test showed a significant relationship between nitrogen and the percentage of exotic plants, and hence available soil nitrogen in the area was an important soil characteristic related with the invasibility of the species found. Nitrogen availability is known to be important in limiting the primary production in terrestrial ecosystems (Kolb and Alpert 2003) and it has been reported that high nitrogen levels in soil increase the probability of invasive plant presence (James et al. 2008; Menuz and Kettenring 2013; Novoa et al. 2014). Hewins and Hyatt (2010) in their study about the flexibility of nitrogen uptake and assimilation mechanisms in biological invasions concluded that if exotic species can respond quickly to increases of nitrogen-related compounds and have a greater affinity for available forms of nitrogen, such as nitrate, they could invade at an accelerated rate. This agrees with what was observed through our results. Urban grasslands as defined by Groffman et al. (2009) can be heavily fertilized for aesthetic purposes and can represent considerable sources of nitrogen, especially if over-fertilized and overwatered. However, urban grasslands also have the potential for N retention as they have an extended growing season compared to native and agricultural ecosystems (Raciti et al. 2008). Designing nitrogen management strategies to control the rate, time, and application of fertilizers in order to reduce nitrate export to surrounding areas can be useful in the control of exotic plants expansion throughout the territory.

A negative relationship was found between abundance-coverage of exotic species with altitude, which was consistent with observations from other investigations (Pauchard and Alaback 2002; Magee et al. 2008; Wu et al. 2010; Menuz and Kettenring 2013). Altitude seems to be a relatively important explanatory variable for the pattern of vegetation distribution observed, because it suggests that lower altitudes are more prone to successful invasion than areas at higher elevations. Pauchard and Alaback (2002) noted that plant invasions were mainly restricted to lowlands because of the hard climate conditions found in highlands and the limited or infrequent access of humans to those areas. Differences in climate conditions along changes in altitude could not be estimated in Potrero de los Funes; however, the access to the highest areas is difficult and this could be limiting anthropogenic disturbance and in turn exotic plant dispersion. Yet, this could change as the urbanization limit moves upward in the Sierras System. Monitoring the extension of the distribution of the exotic plants in an altitude gradient is crucial for the conservation of the communities still unaffected by invasion.

Through the NMDS analysis, it was possible to identify a weak relationship between the pattern of vegetation distribution and soil moisture. Additionally, no significant correlation was found when the Spearman correlation test was applied. Although the presence and abundance of invasive plants is usually favored by the increase of soil moisture (Sanz-Elorza et al. 2006; Richardson et al. 2007; Menuz and Kettenring 2013), it was not the case for the area of study. Even though the authors were able to identify a larger proportion of exotic plant species in areas closer to the river, it might be necessary to obtain a larger dataset to arrive at a more conclusive result regarding the effect of soil moisture and proximity to riparian areas on invasion success.

A weakly positive correlation between pH and the pattern of vegetation distribution was found. Though plant communities with a high proportion of invasive species are usually distributed on acidic soils, which have greater availability of nitrates (Ross et al. 2011; Novoa et al. 2014), that was not the case for Potrero de los Funes as the pH did not vary across the area of study. Similar to pH, the variability in EC was minimal for sampled soils as all soils were classified as non-saline (Peña Zubiate 2002). Other studies have reported a negative association between plant invasion and soil salinity. For example, Perelman et al. (2007) studied the patterns of exotic and native species richness across the Flooding Pampas of Argentina. Their results indicated that native and exotic species numbers decreased along a gradient of increasing soil salinity. However, in our case we found no influence of EC on exotic plants across sites.

No correlation between organic matter and exotic plants was observed in this study. Knicker et al. (2000) observed a connection between invasiveness and organic matter; however, other authors have arrived to different conclusions. Novoa et al. (2014) quantified the changes in soil chemical properties of coastal ecosystems of the Iberian Peninsula caused by the invasion of *Carpobrotus edulis*. One of the parameters analyzed was organic matter content. The results indicated that organic

content was significantly higher in soils invaded by *C. edulis* in comparison to soils with native vegetation in three of the six sampled areas. However, one of the sampled areas showed that organic matter content was similar in invaded and non-invaded areas. They concluded that the connection between content of organic matter and plant invasion depends on the initial characteristics of the invaded ecosystems. In our system, organic matter content showed no significant variations between invaded and non-invaded sites, with litter production being similar in both cases.

Anthropogenic disturbance, nitrate concentration, and altitude were the most important factors influencing the success of exotic plant invasion in Potrero de los Funes. This study provides the first insight regarding the relationships between exotic plant success and site characteristics in a natural-urban gradient ecosystem of the central area of Argentina.

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Supplementary material 1

Phytosociological inventories performed in Potrero de los Funes from 2013-2015
Authors: Romina Paola Nievas, Mirian Roxana Calderon, Marta Matilde Moglia
Data type: measurement
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/neotropical.14.e37633.suppl1